THE GENERA OF THE CANNABACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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CANNABACEAE Endlicher, Gen. Pl. 286. 1837, "Cannabineae," nom. cons.[2]

(HEMP FAMILY)

Rough, mostly aromatic, annual or perennial herbs; stems erect, scandent, or, in perennials, a subterranean rhizome bearing aërial branches, generally ridged or furrowed and either scabrous with long hairs or armed with sharp, rigid, medifixed trichomes often set on multicellular pedestals. Leaves palmately compound or lobed, sometimes simple, petiolate, serrate, generally decussate, but often alternate near the stem apex; lower (abaxial) leaf and leaflet surfaces sparsely or densely covered with hairs and glandular dots, upper (adaxial) surfaces usually crowded with cystoliths and rigid conic hairs with forward-pointing apices; stipules triangular, sometimes fused laterally, persistent. Plants dioecious, rarely monoecious, vegetatively dimorphic or not. Staminate inflorescences loose, erect or ± pendent, axillary, bracteate cymose panicles (thyrses). Staminate flowers small, pedicellate, regular, gynoecium completely absent. Perianth

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[2] Although the orthography of this family name has been disputed, and the spellings Cannabinaceae and Cannabiaceae were frequently used in the past, correctly formed, the name is derived from the stem of *Cannabis, Cannab-*, plus the ending *-aceae.* A recent proposal (Taxon **15:** 211, 212. 1966) to change Cannabaceae to Cannabinaceae (and to modify certain others in the list of conserved family names found in Appendix II of the current edition of the International Code of Botanical Nomenclature) was rejected by ballot during the nomenclature sessions of the XI International Botanical Congress, Seattle, 1969.

uniseriate; tepals 5, greenish or whitish, rarely otherwise, boat-shaped, downy, sometimes glandular. Stamens 5, erect in bud, hypogynous, opposite the perianth segments; anther walls thin, dehiscence longitudinal, basipetal; filaments short, weak; pollen suboblate, triporate, with the tectum thickened around the pores, surface finely granular, ca. 25 μ in diameter. Carpellate inflorescences axillary, basically cymose, spicate, various types of glandular hairs usually present. Carpellate flowers often paired, subsessile, tightly covered or loosely subtended by a bract or bracteole. Perianth uniseriate, thin, undivided, unlobed, at maturity tightly covering nearly the entire ovary. Gynoecium basically bicarpellate, reduced androecium not apparent; style short, apical, central, divided into 2 long filiform stigmatic branches densely covered with soft hairs and caducous soon after pollination; ovary superior, 1-locular with 1 bitegmic anatropous, crassinucellar ovule pendent from near the apex of the locule, the micropyle formed from the inner integument. Fruit a crustaceous achene, covered either loosely or tightly by the perianth. Seed 1; seed coats 2, membranaceous, green; endosperm sparse, fleshy; embryo curved or spirally coiled. Embryo sac development of the Polygonum type, embryogeny of the Onagrad type. TYPE GENUS: *Cannabis* L.

A small family of two genera with several economically important species, native entirely to parts of the temperate Northern Hemisphere, but now widespread throughout the world, although less frequent in tropical regions. *Cannabis* and *Humulus* form a natural unit. They have many characters in common, including a basic similarity in floral morphology, anatomy, and vesture.

A variety of trichome types occurs on members of the family. Nonglandular hairs are mostly unicellular, rarely uniseriate, often with silicified walls, and of three kinds: (1) short, conic hairs with expanded bases that penetrate the leaf mesophyll and frequently contain a single large cystolith of calcium carbonate, occurring on adaxial surfaces, (2) unicellular two-armed hairs on petioles and young axes, and (3) long, lax hairs mostly on abaxial leaf surfaces and stems. Glandular hairs include the following types: (1) unicellular-stalked discoid glands found mostly on abaxial leaf surfaces, bracts, and axes, (2) capitate glands supported by uniseriate or biseriate stalks, most common in the carpellate inflorescence of *Cannabis sativa*, and (3) short-stalked glands with cup-shaped heads, restricted to the carpellate inflorescence of *Humulus Lupulus*.

Species of *Cannabis* and *Humulus* are wind-pollinated. Stigmata have been reported to be exserted from the bracts and receptive 4–5 days before pollen is shed from nearby staminate plants. Staminate flowers are generally pendent at anthesis, but rather than expelling their pollen at once, the anther sacs gradually dehisce basipetally by a longitudinal slit. Initially, pollen sifts through an apical oval opening having the appearance of a pore. A single inflorescence of *Cannabis sativa* has been estimated to produce more than 500 million pollen grains. Dispersal of *Humulus Lupulus* is reported to be facilitated by the adherence of the wing-like

bracteole to the achene. At places in the midwestern United States *Cannabis sativa* achenes have been found in the crops of mourning doves, which may have an active role in the local dispersal of this species.

The Cannabaceae appear to be closely related to both the Urticaceae and Moraceae, with which they share a number of characters. These families may have been derived from the Magnoliales through the Hamamelidales (Cronquist, Takhtajan, Tippo). A relationship with the Malvales, among others, has also been suggested (Thorne and others).

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KEY TO THE GENERA OF THE CANNABACEAE

General characteristics: *erect or scandent herbs, scabrous or armed with rigid climbing hairs, and often with glandular trichomes; leaves palmately compound or lobed, sometimes simple; staminate inflorescence a loose cymose panicle, staminate flowers with 5 free tepals and 5 antitepalous stamens; carpellate inflorescence spicate, carpellate flowers small, perianth uniseriate, continuous, tightly appressed to the ovary, ovary 1, superior, 1-locular, with a single ovule pendent from near the apex of the locule, style branches 2, filiform; fruit an achene covered by the persistent perianth.*

A. Plants erect herbs; leaves palmately divided into long, lanceolate, serrate leaflets; variously provided with trichomes, but two-armed hairs absent from stems or branches and petioles; carpellate inflorescences erect; gynoecium tightly ensheathed by a beaked persistent bracteole with long-stalked glandular hairs. ..... 1. *Cannabis.*

A. Plants scandent herbs; leaves palmately lobed or simple; two-armed hairs present on stems and petioles; carpellate inflorescences pendent; gynoecium loosely subtended by a bracteole with short-stalked and cupulate or sessile glandular hairs. ..... 2. *Humulus.*

1. **Cannabis** Linnaeus, Sp. Pl. 2: 1027. 1753; Gen. Pl. ed. 5. 453. 1754.

Tall (to 5 m.), erect, branched or unbranched, coarse, tap-rooted, weedy annual herbs occurring in waste places, disturbed ground, and alluvial flats; stems obtusely polygonal or round in cross section, ± ribbed or furrowed, often hollow at maturity, scabrous and sparsely covered with resinous dots, especially on the young parts of the axis. Leaves decussate near the base, alternate toward the apex and on branches, palmately compound with 3–15 (usually 5–9) coarsely serrate, long, lanceolate leaflets; the lower surface whitish green, with widely spaced yellow to brownish resinous dots and strigose hairs, the upper surface darker green with large, stiff, bulbous-based conic trichomes; stipules narrowly triangular. Plants dioecious, rarely monoecious except in certain cultivated strains and experimental plants; dimorphic, staminate plants tall, slender, with few leaves in the terminal inflorescence, dying soon after flowering; car-

pellate plants stocky, with a dense crown of leaves associated with the inflorescence, living for several months after pollination. Staminate inflorescences loose cymose panicles, long, if originating from the axils of foliage leaves, short, if from the axils of stipules. Staminate flowers pedicellate, small, pendent at maturity, caducous soon after shedding pollen. Tepals greenish, rarely purplish, quincuncial in bud and widespread at anthesis. Anther walls thin, bearing glandular hairs at the junctures of anther lobes; pollen sacs 4 (bilocular at anthesis); filaments flaccid. Carpellate inflorescences congested series of axillary false spikes; the main axis, leaves, petioles and bracts associated with carpellate inflorescence often densely covered with resinous capitate or ± sessile glandular hairs. Carpellate flowers sessile or nearly so, ensheathed by a glandular, beaked perigynal bracteole and subtended by a bract (stipule?). Perianth papery, continuous, closely appressed to the ovary. Fruit an ovoid, somewhat compressed achene with the perianth persistent, reticulate, and often mottled with brown; pericarp 5 layered, the inner palisade layer the thickest. Seed 1, ovoid; perisperm 1 cell-layer in thickness; endosperm fleshy, with a chalazal haustorium; embryo curved, U-shaped, flexed in the region of the epicotyl, with the radicle and cotyledon tips pointing toward the micropylar end of the seed (ovary apex); $2n = 18 + XX$ or XY. TYPE SPECIES: *C. sativa* L. (Ancient Greek and Latin name for hemp, said to come from Arabic, *kinnab*, or Persian, *kannab*.) — HEMP, MARIJUANA.

A genus of one (or perhaps more) species, originally indigenous to temperate parts of Asia, probably to the desert region immediately to the south and east of the Caspian Sea, but now occurring as an adventive or naturalized weed throughout most of the world. *Cannabis sativa*, a decided nitrophile that grows well in close association with man and his wastes, is widespread in the United States and most frequently collected in Kansas, Nebraska, Iowa, and Illinois. It is known from only a few stations in the Southeast but may be more abundant than herbarium specimens and literature reports imply.[3] *Cannabis ruderalis* Janisch. (Učen. Zap. Gos. Saratov. Univ. 2(2): 14. 1924), a possible second species occurring in Central Asia, southeastern Russia, and as a weed in eastern and Central Europe, is reported to differ from *C. sativa* in size and achene characters. Most authors accept only one species, and whether the diagnostic characters of *C. ruderalis* are distinct and do not overlap the extensive variability of *C. sativa* remains to be worked out carefully.

Cannabis sativa has been much used as an experimental plant. Interest was focused early on monoecious hemp plants and the "reversion" of carpellate plants to staminate ones and vice versa. For example, seeds planted in summer at Columbus, Ohio, yielded about equal numbers of carpellate and staminate plants, but seeds from the same lot sown indoors

[3] Haney and Bazzaz plausibly relate the apparent rarity of *Cannabis sativa* in the southeastern United States to derivation of naturalized hemp in North America mostly from temperate European and Chinese fiber strains which are ill adapted to growing under environmental conditions present in the Southeastern States.

in December, gave a crop in which more than three-quarters of the carpellate plants produced intersex or pure male flowers and a similar proportion of the staminate plants occurred with intersex or pure female flowers. After the discovery of photoperiodic responses in plants about 1920, it was realized that hemp was a short-day plant in which sex reversal was correlated with exposure to ever shorter periods of light. Other factors, including temperature and available soil nutrients, apparently also exert some control. However, the genetic basis of sexuality in hemp is still not fully understood. Although environment was originally considered to have the major role and Mendelian inheritance to be inconsequential, different workers have demonstrated the presence of a heteromorphic chromosome pair in staminate meiotic material from several dioecious strains. A heteromorphic pair has been less convincingly shown in certain monoecious strains. In dioecious hemp, sex determination is thought to be under an XX = ♀ and XY = ♂ system, and derived monoecism has been explained in two ways: monoecious plants are all XX, and variation in sex expression is due to heterozygous genes on the X-chromosomes and autosomes; or XX, XY, and YY monoecious plants can occur, but only autosomes determine sex. Unfortunately, somatic karyotypes have been imperfectly investigated.

The morphology of the spicate carpellate inflorescence of hemp has been interpreted in several ways. Buds are reported to occur in the axils of both stipules and leaves, and, according to Camp (1932), stipular buds (two at each node) give rise to short determinate branches bearing single flowers, whereas the true axillary bud produces an indeterminate branch bearing leaves and stipular flowers but no secondary axillary branches. Bud primordia are visible in the axils of reduced leaves borne on the axillary branch, but suppression is broken only under extraordinary conditions. In an alternate interpretation (see Hayward, 1938) a pair of flowers, each subtended by a stipule, is claimed to arise in a leaf axil. A secondary branch, also issuing from the leaf axil, bears another leaf with stipules and flowers, and this, in turn, produces an axillary branch of the third order. The staminate inflorescence is composed of a main indeterminate axis bearing secondary branches from both the axillary and stipular buds near the base, but only from the stipular buds toward the apex (Camp, 1932). The staminate inflorescence of hemp is called a panicle or raceme by most authors, but the side branches are clearly cymose.

Zander has studied the poorly differentiated, unbranched, and inarticulate laticifers that occur in the stem of hemp. He concludes that "the anatomical behavior and developmental history of hemp laticifers are different in comparison with the rest of Moraceae" (transl.).

Three economically important products are obtained from *Cannabis sativa*. Perhaps least significant (except in Russia) is a drying oil pressed from the fruits. The oil is used as a substitute for linseed oil in paints and varnishes and occasionally in soap making. After expressing, the "seed"-cake may be fed to cattle. In parts of eastern Europe and Russia roasted hemp "seeds" are eaten by humans, and in the United States *Cannabis*

achenes are sold in seed mixtures prepared for cage-birds and outdoor bird-feeders. At one time uneaten achenes from such mixtures were a major source of spontaneous hemp plants, but now the "seeds" are sold only after the embryos have been killed.

In many parts of the world hemp is grown on a commercial basis for fibers which are made into ropes, twines, bags, and webbing. Clothing was once made from the finer grades, and the strong, durable fibers of hemp were used extensively for sail cloth. A tarred caulking material, oakum, is produced from shorter fibers and tow. Hemp is most successfully grown for fibers on rich, humified loam in a mild, humid climate. Individual fibers are about a centimeter long and occur in two zones in the stem. The outer, primary fibers are longer and thicker walled than the inner, secondary fibers, and both series are separated by several layers of parenchyma, a feature that enables the isolation of the primary fiber-bundles by retting. In general, internode and fiber-bundle length are in direct proportion, and tall cultivars with fewer nodes are sought. Staminate plants produce the finest grade of fibers. Because staminate plants die soon after shedding pollen, while carpellate plants live until the fruits mature, breeding programs have been directed toward producing either monoecious strains with the tall growth-habit of the staminate plant or uniform-ripening dioecious races. Colchicine-induced tetraploid strains, which give a greater yield of higher quality fiber than normal diploids, are grown to some extent. Hemp agriculture in the United States first started on a limited basis in New England, in 1632, with seeds brought to the Colonies from England. In the 1800's, particularly during the midcentury years, hemp was extensively grown in the Bluegrass Region of Kentucky from seeds of Chinese origin. During the 1850's, 75,000 tons were harvested annually in the United States, but production had dropped to 5000 tons or less by the early 1900's. Acreage in hemp dramatically increased during both World Wars. In 1943, as a response to the inaccessibility of Manila hemp, nearly 63,000 tons were produced. All hemp fiber used in the United States in recent years has been imported, generally from European sources.

The hemp plant is the source of an important narcotic drug. Its effect on humans, although at present mostly lacking scientific documentation, seems to be to induce a general state of euphoria, frequently broken with periods of depression, and often accompanied by vivid mental imagery. The drug is apparently widely used throughout the World, in spite of severe penalties. There is some evidence that the use of hemp drugs in the United States started about 1910 in New Orleans. The narcotic principle occurs in the resinous material that accumulates most abundantly on tissues of the carpellate inflorescence. Among the numerous compounds isolated from the resin in recent years, the dibenz-α-pyrans, Δ^1- and Δ^{16}-*trans*tetrahydrocannabinol (THC), have been found to be the major agents of intoxication in man. At present, tetrahydrocannabinols are reported from no other plant.

Methods of taking the drug vary somewhat from culture to culture.

In the United States, *marijuana* is a mixture of the resin and various plant fragments, generally from the carpellate inflorescence, while *hashish* is a term restricted to the pure resin. Both forms are most often smoked. In India the resin may be eaten or drunk in various carriers, especially milk. The word *assassin*, taken directly from the Arabic *hashshāshīn*, *hemp eaters*, entered the English language at the time of the Crusades. The hashshashins were a group of murderers who were supposed, perhaps erroneously, to have carried out their missions, while intoxicated by hashish.

The largest amount of resin is produced by flowering carpellate plants in hot, dry climates. An increase in humidity lowers production, and stems, lower leaves, and seeds contain the least amount of resin. Plants grown in India have been reported to contain 20 per cent resin, those from Mexico 15 per cent, and samples from Kentucky and Wisconsin 8 and 6 per cent, respectively. There are conflicting statements in the literature about the occurrence of THC in carpellate and staminate plants of different geographic origin and in strains grown for fibers and oil. Selection of high-yield fiber or oil cultivars apparently may result in a loss of THC, in spite of the retention of high resin-production. Staminate plants from certain strains lack THC, but the intoxicating principle may occur in male plants of other cultivars. To date, a thorough analysis of the resin from wild self-seeding types and cultivated dioecious and monoecious strains grown in various parts of the World for fiber, oil, or the drug has not been made. Gas chromatographic methods would be useful in such a study.

Forensic identification of marijuana is based on microscopic examination of the sample, in conjunction with one or several chemical tests applied to a petroleum-ether extract of the resin. The glandular and non-glandular hairs occurring on the upper and lower leaf surfaces, petioles, and bracts of the inflorescences of both sexes are considered distinctive, especially when compared with an authenticated specimen. Since the cystoliths of *Cannabis sativa* are composed of calcium carbonate, addition of dilute hydrochloric acid will cause a slight effervescence, which is visible through a low-power microscope.

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2. **Humulus** Linnaeus, Sp. Pl. 2: 1028. 1753; Gen. Pl. ed. 5. 453. 1754.

Rough, scandent and dextrorse-twining annual or perennial herbs of river and stream bottoms, thickets, hedgerows, roadsides, and other disturbed sites; with long taproots, or, if perennial, with a massive rhizome and abundant adventitious roots; aërial stems weakly ridged, often hexagonal in cross section, rigid two-armed climbing hairs frequent near the apex and often on multicellular emergences; axillary branches mostly from upper nodes. Leaves generally decussate, or alternate when associated with an inflorescence, sometimes simple and cordate but more often palmately lobed, serrate; venation strictly palmate; petioles with two-armed trichomes; lower leaf surfaces with clear or yellowish resinous dots and widely spaced hairs on lamina and major veins, upper surfaces densely covered with cystoliths and short, rigid conic hairs; stipules lanceolate, two per petiole or coalesced laterally into one. Plants dioecious, rarely monoecious when growing in nature. Staminate inflorescences axillary, sometimes terminal, erect or ± pendent, many flowered, loose cymose panicles. Staminate flowers pedicellate, small. Tepals greenish, bearing on the abaxial surface glandular dots and occasionally long, rigid trichomes. Glandular dots at junctures of the anther lobes either present or absent. Carpellate inflorescence spicate, consisting of a series of ovate or acuminate stipular bracts and bracteoles subtending solitary or paired flowers; bracts and bracteoles pubescent or ciliate, with sessile glandular dots or short-stalked cupulate lupulin glands on abaxial surfaces. Carpellate flowers with short pedicels, borne in the axil of a bracteole which at maturity is large and either brown and membranaceous or ± foliar and green, sometimes reddish pigmented. Perianth continuous, thin, appressed to the ovary, either covered with lupulin glands or not. Fruit a lenticular or ± round achene, tightly or loosely ensheathed by the brownish or sometimes mottled persistent perianth; pericarp crustaceous. Seed 1; embryo coiled into a tight spiral, cotyledons long, radicle pointing toward the micropyle. Type species: *H. Lupulus* L. (Late Latin name for this plant, from Old Slavic.) — HOP.

A genus of two species native to portions of the North Temperate Zone but now widely cultivated, escaped, or naturalized throughout temperate areas of both hemispheres. Originally indigenous to eastern Asia (China, Taiwan, Manchuria, Korea, and Japan), *Humulus japonicus* Sieb. & Zucc.[4] is naturalized in eastern North America southward to North Carolina, South Carolina, and Tennessee. It differs from *H. Lupulus* L. in many characters, among which the occurrence of ciliate hairs on the margins of the bracteoles and stipular bracts, the absence of lupulin glands, and the presence of from 5 to 7 leaf lobes (*vs.* 0–3 [5] in *H. Lupulus*) are the most readily observed. Wild *H. Lupulus* is disjunct in the Northern Hemisphere. It occurs in Japan, a part of North America, and from central Asia to southern Europe, a range that appears to fit one of the Arcto-Tertiary distribution patterns. The populations in each region have been considered distinct species, although recent work indicates that only subspecific differences exist between them. *Humulus Lupulus* presently is found throughout most of the United States and southern Canada, but the actual range of the native North American hop, which Nuttall, in 1848, named *H. americanus* (based on a Gambel collection from New Mexico), remains unknown. The early introduction of *H. Lupulus* from Europe for use in brewing and its subsequent escape and spread have made it difficult to decide whether a particular plant is native or introduced. However, pollen of *H. Lupulus* has been found at several sites in the upper Midwest in lake sediments deposited long before the presence of European man in the New World. Future detailed analysis of postglacial sediments from elsewhere in North America could ultimately solve the problem of the pre-settlement distribution of the native hop on this continent.

The spicate carpellate inflorescence of *Humulus* consists of a condensed primary axis bearing reduced secondary branches (Ehara, 1955; Hamaguchi, 1955). Internodes, although shortened, are clearly discernible. In *H. Lupulus* two flower pairs normally occur per node, each pair being subtended by a bract and each individual flower by a bracteole. Peduncles and pedicels are short, and the flowers are subsessile. The nodal flower clusters are interpreted as cymes in which the third (first opening) flower of each pair and the flower or branch between the pair are suppressed. Infrequently a reduced leaf is found at certain nodes between the two enlarged bracts, indicating their homology with stipules. Stipular bracts generally have pointed apices, while bracteoles are obtuse. The

[4] Merrill (Trans. Am. Philos. Soc. **24**: 138. 1935) contends that *Antidesma scandens* Lour. (Fl. Cochinch. **2**: 617. 1790) is unmistakably the species widely known as *Humulus japonicus* Sieb. & Zucc. (Abh. Akad. Wiss. München **4**(3): 213. 1846; also issued with different pagination as Fl. Jap. Fam. Nat. **2**: 89. 1846). If Merrill is correct, his combination, *Humulus scandens* (Lour.) Merr., should be adopted. Unfortunately, Loureiro's description, based on only a staminate plant, is superficial and mentions glabrous leaves and unarmed stems, two characters that are difficult to attribute to *H. japonicus*. Further, since the specimen upon which Loureiro based his description apparently has not been preserved (see Merrill, *loc. cit.*), the applicability of the name *H. scandens* seems open to question.

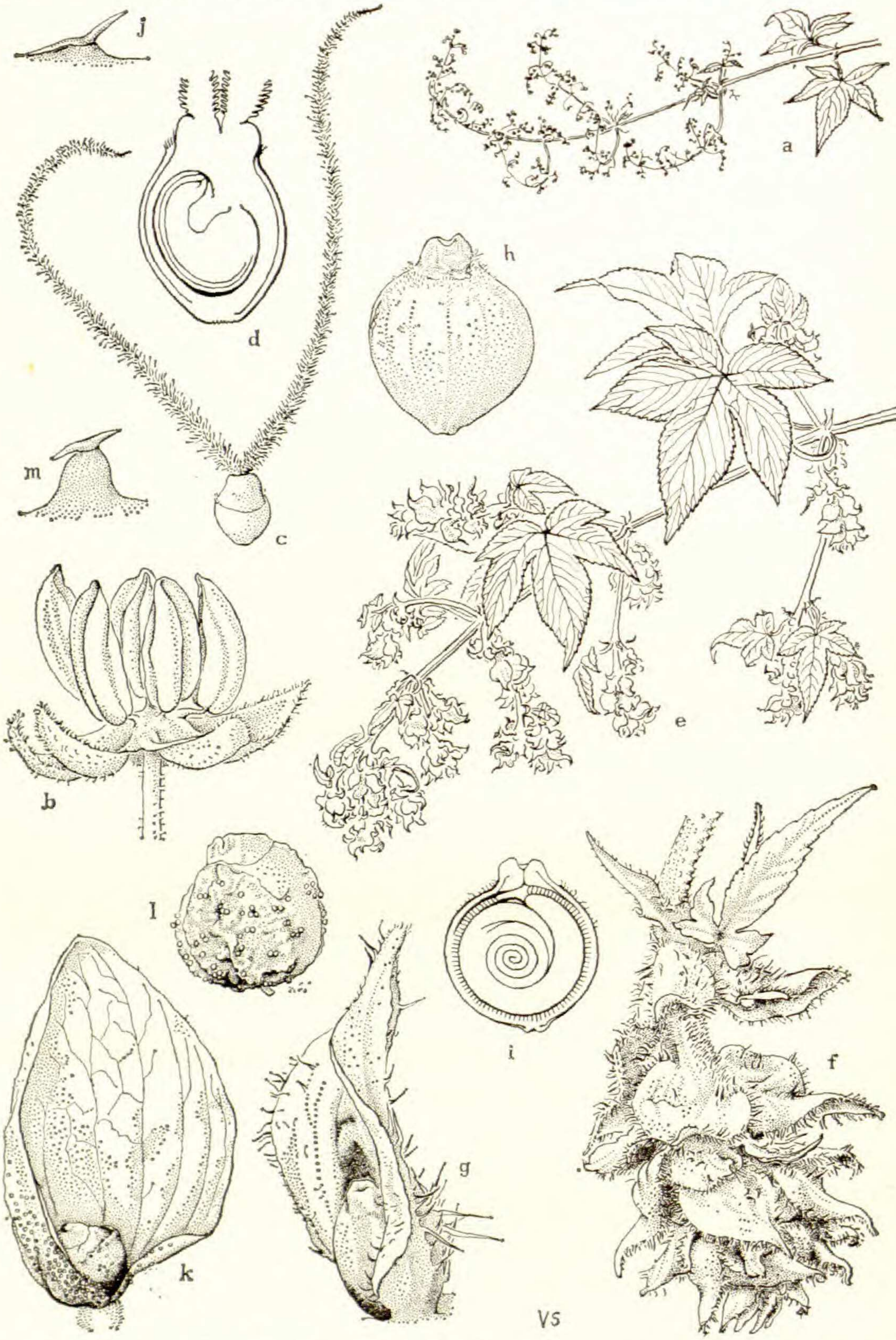

FIG. 1. **Humulus.** *H. japonicus*: a–j. a, terminal staminate inflorescence, × 1/4; b, staminate flower, × 10; c, carpellate flower with partly developed perianth, × 12; d, longitudinal section of ovary showing ovule, style branches mostly removed, × 20; e, terminal carpellate infructescence, × 1/2; f, fruiting spike showing pointed stipular bracts and bracteoles with blunter apices, × 2; g, nearly mature achene in axil of bracteole, × 5; h, mature achene with tightly appressed perianth, × 6; i, achene with embryo in diagrammatic longitudinal

carpellate spikes of *H. japonicus* and *H. Lupulus* are morphologically similar except that in the former only one flower (with its associated bracteole) occurs in the axil of a stipular bract. Sterile bracts are commonly present at the base of the inflorescence.

The diploid chromosome number in *Humulus Lupulus* is 20, and Winge in 1923 first demonstrated a heteromorphic pair of sex chromosomes (XY) in staminate plants of European origin (see Ono & Suzuki, 1962). Although carpellate plants of this species apparently uniformly have a homomorphic pair of sex chromosomes (XX), more recent research on the chromosomal makeup of staminate hop has shown considerable variability which seems to be correlated with the geographic origin of the plants. Working with the wild hop of Japan, Ono (1955, 1962) found that the sex chromosomes almost invariably took multiple forms consisting of four or six chromosomes. Both types, the more frequent tetravalent and the rarer hexavalent, presumably have arisen by reciprocal translocations between the original XY chromosome pair and certain autosomes. At meiosis, components of the sex chromosome complex conjugate end to end. Cytological studies on staminate European and American hops have been less extensive, but, in general, the simple XY type seems to prevail in plants from Europe, while in American samples homomorphic XY males, heteromorphic XY males (X length: Y length = 10:8 instead of 10:5 as in the European hop) and tetravalent complexes have been observed. Sex chromosomes have been found in *H. japonicus* also, but instead of an XY mechanism, the staminate plant has a $2n$ chromosomal complement of 14 autosomes and 3 sex chromosomes, Y_1XY_2. The Y chromosomes are heterochromatic for most of their length. During anaphase I of meiosis in staminate plants, 8 chromosomes go to one pole and 9 go to the other. Carpellate plants have a $2n$ number of 14 + XX.

Bracteoles, perianths, and, to a lesser degree, stipular bracts of the mature fruiting spike of *Humulus Lupulus* are covered with large cup-shaped glands filled with a yellow resinous substance, lupulin, that is used to impart flavor and aroma to beer. Bacteriostatic agents in lupulin also inhibit the growth of spoilage bacteria, while permitting yeast to develop freely and ferment the wort, a mixture of sugar (obtained by enzymatic conversion of starch from various grains) and water. Hops may be added to the wort while it is being boiled prior to the onset of fermentation or to the final beer in the storage tank. In the former case, the bittering substances are formed from the resin constituents during boiling, while in the latter the flavoring is derived from essential oils in the resin.

Lupulin is composed of soft and hard resins, but only components of the soft resin apparently contribute to a beer's flavor. The aroma of beer

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section, endocarp hatched, × 6; j, rigid 2-armed trichome from petiole, × 25. *H. Lupulus*: k–m. k, mature achene in axil of bracteole, × 4; l, mature achene with persistent ± inflated perianth and lupulin glands, × 10; m, rigid 2-armed trichome from petiole on multicellular pedestal, × 25.

derives solely from essential oils, a distinct group of compounds. Soft resin can be separated into α-acid, β-acid, and uncharacterized fractions, each category containing a number of distinct organic compounds. Isomerization of the α-acids during boiling yields water-soluble, bitter-tasting isohumulone and its analogues, which strongly inhibit the growth of Gram-positive bacteria. Lupulone in the β-acid fraction is also bacteriostatic. The percentage of cohumulone in the α-acid component has been shown to vary in amounts which correspond to groupings or morphological features recognized as characteristic of hops either native or long-cultivated in England, the European continent, and America (Davis & Burns, 1962).

The cultivated hop was introduced into North America in 1629, and by 1650 commercial crops were being harvested in Virginia and New Netherlands. During the 1800's and early 1900's New York was an important region of hop cultivation, although following the Civil War, the industry began to spread westward through Pennsylvania to Wisconsin. In the United States today the leading areas of hop production are Idaho, Washington, Oregon, and California, where three principal varieties are grown. The first, the English hop, was obtained by crossing a wild carpellate plant from Manitoba with an English staminate plant, and the second, the Fuggle hop, was selected from seedlings raised in England. The origin of the third, Cluster hops, is less certain. The Late Cluster type originated during Colonial times on the eastern seaboard, perhaps as a seedling from an English variety then in cultivation, while the Early Cluster type was derived as a bud sport directly from the Late Cluster hop. At the present time the most widely grown hops in the United States are the Cluster varieties. Hops are also cultivated in Canada, Europe, northern India, China, Manchuria, Japan, South Africa, southeastern Australia and Tasmania, New Zealand, and southern South America. Pollination is not necessary for the development of the spike and lupulin glands, so staminate plants are rarely raised in hop yards, except for breeding purposes. Rhizome cuttings are used for propagation.

Hops require a well-drained, nitrogen-rich soil and will not tolerate sharp temperature fluctuations or excessive rainfall during the growing season. Late summer dryness is necessary for proper maturation of the spikes, which must be picked within a few days of full ripeness, otherwise they are prone to shattering, and the lupulin quality is inferior. After harvesting, hops are dried in warm air kilns for several hours, cooled or cured in another building for about a week to equalize moisture content in the various pickings, baled, and marketed.

In former times hops have been used medicinally as multipurpose tonics and to treat certain types of epidermal sores and irritations, usages perhaps related to the bacteriostatic quality of the resin. In Scandinavia phloem fibers from the aërial stems of *H. Lupulus* are made into twine and cloth to a limited extent. *Humulus japonicus* is occasionally used as an ornamental plant.

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